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On new species in a new earthworm genus from Puerto Rico¹

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ABSTRACT. A new genus of earthworms, *Estherella* (family Glossoscolecidae), with new species *montana* (type species) and *nemoralis*, is described from Puerto Rico, and its remarkable structural modification is discussed.

A seemingly impossible evolutionary modification was shown by several worms received 25–30 years ago. Immaturity, amputation, maceration, and paucity of specimens prevented completion of species descriptions to desired standards. Unfortunately subsequent material never became available. Various attempts to secure it were futile. This contribution now is proffered in hope of awakening interest in: 1) An evolutionary development that some zoologists categorically maintain is impossible. 2) The mostly unknown earthworm faunas of Caribbean Islands.

Glossoscolecidae *Estherella* gen. nov.

Definition. Digestive system, with a gizzard in iii, three pairs of calciferous glands in v–vii, each gland sausage-shaped, vertically placed alongside gut, with a short duct from dorsal end opening into esophagus just lateral to the supra-esophageal vessel, intestinal origin in region of xix–xx, with a lamelliform typhlosole, without caeca and supra-intestinal glands. Vascular system, with a single dorsal trunk aborted in front of hearts of iv, complete ventral and subneural trunks, the latter adherent to parietes, a supra-esophageal trunk in v–xiv, paired latero-esophageal trunks

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in iii-ix with connectives to supra-esophageal in v-vii. Hearts, in iv-vii lateral, in viii latero-esophageal. Nephridia, holoic and vesiculate. Nephropores, obvious, in a regular longitudinal rank on each side in region of *CD*. Pigment, none. Septa, present from 3/4. Prostomium, none, replaced by a protrusible proboscis. Setae, eight per segment, in regular longitudinal ranks.

Quadrithecal, spermathecae adiverticulate, pores in region of *CD*, at 5/6-6/7.

Type species, *E. montana* n. sp.

Distribution. Puerto Rico.

Estherella montana sp. nov.

Puerto Rico, El Yunque Mountain. Wet cloud forest at \pm 2500 feet, May 1938, 3-0-0. P. J. Darlington per G. E. Pickford. (Mus. Comp. Zool.) About 2200 feet, an anterior fragment, C. W. Richmond & L. Stejneger. (U. S. Natl. Mus.)

External characteristics. Length, 50-60 mm (juveniles), 175 mm (posterior amputee of 148 segments). Diameter, 4 mm (juveniles), 12 mm (amputee). Segments of 54 mm juvenile, 188. Color, white (long alcoholic preservation). Peristomium, much shorter than ii but of about the same appearance externally as subsequent segments. Intersegmental furrows, distinct. Segmental length, gradually increasing posteriorly to region of vii-ix. Secondary annulation, a presetal and a postsetal secondary furrow in each of ix-xxvi, postsetal secondaries unrecognized behind xxvi. Nephropores, obvious, present from ii, well behind intersegmental furrows but usually less than half way toward segmental equators, at or near *C*. Setae, paired, ventral couples first certainly recognizable in v, lateral couples in region of xv, in region of xxx *CD* slightly $< AB$ much $< AA < BC$, posteriorly $AA \text{ ca.} = BC$, still further back $AA > BC$. Dorsal pores, none.

Quadrithecal, spermathecal pores, minute, superficial, in *CD*, at 5/6-6/7. Other genital apertures, unrecognizable. Genital tumescences, transversely and shortly elliptical, indistinctly delimited, each with two circular areas of epidermal translucence at center of which is a follicle aperture, *a,b/xv-xxiv*. Region of *AA*, rather deeply depressed through xv-xxiv.

Internal anatomy. Septa, 4/5-13/14 thickly muscular to muscular, funnel-shaped, large, apices well posteriorly, 14/15 and following septa slightly strengthened by muscular fibers. Septum 3/4, a delicate transparent membrane bearing on its posterior face

one pair of nephridia and on its anterior face two other pairs of tubules, with insertion on gut immediately behind gizzard. Pigment, if once present in body wall, completely leached by preservative. A large, empty canal, elliptical in cross section, apparently completely circumferential, in anterior portion of body wall in each of i-x. Canal size, decreasing posteriorly. Brain, in ii. Nerve cord sheath, massively muscularized (Fig. 1) anteriorly but so as to leave a greyish translucent line visible at mD and mV in the cord between segmental ganglia (Fig. 2).

Buccal cavity, in i dorsally of small juveniles, seemingly provided, though only temporarily, with a suckerlike pad somewhat resembling the withdrawn and depressed condition of the prostomium in various megadriles, in ii dorsally with a circular aperture into a tunnel containing a presumably protrusible proboscis 1-2 mm long. Gut from level of intersegmental furrow 2/3 to septum 4/5, *ca.* 30 mm long, sigmoid, comprising a pharynx (4 mm long), a bulb (5 mm thick dorsoventrally and with a glandular chamber anteriorly), a slender esophagus (14+ mm long) with closely crowded, low longitudinal ridges on its inner wall, a sort of conical crop (5 mm long) with circular ridges on its inner wall, and a powerful gizzard (6 mm long) referable to iii.

Calciferous glands, in contact with each other mesially under the gut, in vii ducts longer but concealed by adherence of 7/8 (near apex of its funnel) to the gut. Typhlosole, present from region of xxiv-xxvi, 10 mm high (3 mm, small juvenile), rolled up on itself like a scroll, ending in region of 125th segment (132d of 188). Lateral typhlosoles, not lamelliform, rounded and protuberant ridges in first one or two typhlosolar segments.

Ventral blood vessel, high up in coelom and near gut in v-xi at least. Extra-esophageals, interconnected by a transverse vessel just in front of 4/5 and just under the ventral trunk, anteriorly passing up and branching among nephridia associated with 3/4. Supra-esophageal, with a large branch on each side in v and vi that bifurcates, one branch to a calciferous gland near the duct, the other passing down along anterolateral aspect of the gland to an extra-esophageal trunk, connected also with extra-esophageals by a pair of vessels, seemingly on posterior face of 7/8 but mostly within the septum. Hearts, of iv-vii slender and lateral, of viii apparently latero-esophageal—posterior bifurcations to dorsal trunk slender and empty, anterior branches filled with blood and obviously joining the supra-esophageal.

Nephridial ducts (of anterior segments), passing down through longitudinal muscle layer and then turning forward to cross the circumferential intra-parietal canal, thence anteriorly widened and with more opaque (muscularized?) wall.

Spermathecae, rudimentary, adiverticulate, within the longitudinal muscle layer.

Remarks. Small juveniles are assumed to be of the same species as the large worm from the same mountain.

Rudimentary state of the spermathecae and absence of macroscopically recognizable gonads, funnels, and seminal vesicles, indicate that even the large worm was juvenile though maximum diameter for the species may have been attained.

The parietal insertion of the delicate septum 3/4 had become unrecognizable presumably as a result of pinning out the specimen after a longitudinal incision had been made near the mid-dorsal line.

Any connection between nephridial ducts and the circumferential intraparietal canals would have been too small to recognize in dissection, and microtome sections were unsatisfactory. The canals were crossed diagonally by delicate fibers (or septa?). Similar canals had been observed at least once before, but records were destroyed during World War II.

Abortion of dorsal trunk in front of hearts of iv and posteriorly in that segment was found in each dissected specimen considered herein. That and other characters already mentioned in the generic definition do not need mention again in species descriptions.

Photographs of nerve cord sections were provided by Prof. E. Carpenter.

E. nemoralis sp. nov.

Puerto Rico. Luquillo Forest (Caribbean National Forest), La Mina Recreational Area, at 1800 feet, February 22, 1947, 2 macerated specimens (several younger specimens possibly of the same species, also macerated.) R. Kenk. (U. S. Natl. Mus.)

External characteristics. Length, 250 mm. Diameter, 9 mm. Segments, 220 (at 195/196 a tail regenerate with terminal anus). Color, possibly red originally, even after long alcoholic preservation dorsum with a slight reddish tinge except in regenerate. Nephropores, obvious, present from ii, in CD. Setae, closely paired throughout, $AB = CD$, $AA > BC$, DD ca. $= \frac{1}{2}C$, ventral

couples of some segments modified (? but genital tumescences not recognized).

Clitellum, perhaps represented by a dark brown coloration in xv-xxii, xxiii/eq, which is conspicuously lacking in a small area around each nephropore, no epidermal tumescence recognizable. Quadrithecal, pores minute, superficial, each at center of a small tubercle at C and at or immediately in front of 5/6-6/7. Female pores, postsetal in AB of xii(?).

Internal anatomy. Septa, 4/5-6/7 very thickly muscular, a transparent, funnel-shaped membrane bearing three pairs of nephridia inserted on the gut just behind the gizzard almost immediately in front of 4/5 presumably being 3/4, 7/8 lacking or else inserted on parietes over intersegmental furrow 8/9.

Calciferous glands, without a central lumen but with a honeycomb appearance in cross sections, each with a small distal appendage.

Supra-esophageal, bifurcating posteriorly in xiv, giving off two pairs of vessels, one immediately behind the other and both just in front of the septum in each of v-vii, the posterior of each pair giving off branches to the calciferous gland and ventrally joining the extra-esophageal trunk of its side, the anterior vessels passing onto stalks of calciferous glands and down through the glands into the terminal appendages. Extra-esophageal, first visible in region of 3/4 as a result of union of several large vessels, with several branches to each calciferous gland of its side. Subneural trunk, large, zigzag-looped, closed ends of loops visible beyond both sides of the nerve cord, bifurcating just in front of subpharyngeal ganglion (one specimen) or in region of xvii (one), each branch passing anteriorly in a zigzagged course lateral to the cord but connected with its twin on the opposite side by numerous transverse vessels. Ventral trunk, high up in coelom as in *E. montana*. Hearts, large, two pairs, possibly latero-esophageal and attributable to viii-ix (?).

Testis sac (or sacs?) filled with coagulum, surrounding or including hearts belonging in viii (?).

Spermathecae, sessile, ducts confined to body wall, ampullae small, protruding only slightly into coelomic cavities of vi and vii.

Remarks. Intersegmental furrows, in spite of the maceration, are distinct, and septa 4/5-6/7 are inserted on the parietes directly over intersegmental furrows 4/5-6/7.

Thickness of the subneural trunk is greater than that of the nerve cord even in regions of segmental ganglia.

The cuticle was loose and setae had been pulled out of their follicles.

Repetition in the description of characters shared identically with *E. montana* seems unnecessary. Mention should be made of the fact that a proboscis and circumferential parietal canals were not seen.

This species is distinguished from *E. montana* by absence of the marked muscularity in the nerve cord sheath.

Estherella sp.

Puerto Rico. Luquillo Forest (Caribbean National Forest), La Mina Recreational Area, 1800 feet, February 22, 1947, 1 macerated specimen. R. Kenk. (U. S. Natl. Mus.)

External characteristics. Size, 150 by 7 mm. Nephropores, obvious, present from ii, in *CD*. Setae, paired throughout (ventral couples modified in some clitellar segments?).

Clitellum, xv-xxii (and xxiii?). Tubercula pubertatis, longitudinal bands of translucence, just lateral to *B*, each demarcated laterally by a deep furrow. Female pores, postsetal in *AB* of xii(?).

Internal anatomy. Male funnels, one pair, iridescent, imbedded in coagulum apparently also containing hearts of viii and possibly in sacs (or a testis sac?). Spermathecal ampullae, spheroidal, without spermatozoal iridescence, slightly protuberant into coelomic cavities from the angles of septal insertions and parietes.

Remarks. Setae had been pulled out of their follicles as in the types of *nemoralis*. Gonads and female funnels were not found. Structure, so far as could be determined, is the same as is shared by the two preceding species.

The reason for anticipating a third species is the maturity at a size smaller than is expected for the other two.

SYSTEMATICS

Cephalization has had little attention from oligochaetologists and perhaps least of all in connection with a family in which one manner of evolutionary modification seemingly had its most extensive, as well as perhaps least appreciated development.

Metamerism in oligochaetes sometimes has been said to be homonomous, *i.e.*, similar throughout the body. Typically, the soma is in anteroposterior segments, each of which, at least in earlier stages of evolution, has four pairs of setae, a pair of

nephridia, and a section of the gut. Such a segment is demarcated externally from each of its two contiguous neighbors by intersegmental furrows, circumferential lines where the epidermis is thinnest. Internally, a segment is delimited by transverse partitions, the intersegmental septa. The latter, typically, are in exactly the same anteroposterior levels as the intersegmental furrows. Peristomium and periproct, according to such definitions, are not segments, though for practical purposes are counted as such.

Differentiation in a relatively short anterior portion of the soma of special digestive organs such as gizzards, calciferous glands, etc., and localization of gonads are aspects of oligochaete cephalization so universal as not even to have been thought to be involved. More usually considered were abortions, as of follicle and nephridial anlage, and disappearance of septa and intersegmental furrows, *i.e.*, those structures existence of which enables recognition of segments. Slight (or at least seeming) displacements of septal insertions on the parietes have been known for some time. Recognized but recently (Gates, 1943: 92) was a seemingly posterior dislocation of the parietal insertion of septum 9/10, in *Pontoscolex corethrurus* (Müller, 1857), to a position over site of intersegmental furrow 10/11. Failure to recognize that dislocation was responsible in part for assignment of certain organs in systematic descriptions to wrong segments. How many other errors of that sort were made in past characterizations of glossoscolecid remains to be learned.

Appearance of deep, secondary, and even tertiary furrows hardly distinguishable from the primary intersegmentals, in association with abortions of setae and nephridia, also has been responsible for errors in determination of organ locations. Such mistakes are unfortunate, as knowledge of exact organ position along the anteroposterior axis is of first importance for megadrile systematics and phylogeny. Absence of data as to segmental location of the gonads in the Puerto Rico species is not so regrettable as would formerly have been thought since it is now known that "andry" often, and sometimes even "gyny," does vary intragenerically.

Fortunately, the worms now under consideration, in spite of the poor condition, are free of external modifications that might lead to wrong determinations of organ locations. Setal follicles, to be sure, have been aborted in some of the anteriormost segments, but compensation is provided by the nephropores which not only are all present but also are obvious. Secondary and

tertiary furrowing is lacking, and the anterior segments are clearly demarcated by unmistakable intersegmental furrows. The first two segments have the normal appearance of externally exposed epidermis. No evidence was found for the existence of an actual pre-oral vestibule comprising one or two rudimentary segments no longer exposed regularly to the external environment. Furthermore, the unusual condition next to be discussed characterizes every individual of two, or possibly even three, species. Individual abnormality or defective anterior regeneration accordingly cannot be invoked as was contended when a single Panama specimen was described (Gates, 1968) with a similar condition.

The powerful gizzard, being in front of a membrane that, because of nephridial relationships, must be regarded as septum 3/4, is unusually anterior. With the single exception of the above-mentioned Panama species, a megadrile gizzard has not hitherto been found in front of segment v and often is further back in the esophagus. Other organs also are too far forward. The last pair of hearts is in viii, whereas the first pair of real hearts usually is in ix. Calciferous glands are present in v only in the Panamanian *Thamnodriloides yunker* Gates, 1968. Lastly, testes are at least two segments in front of where they would normally be expected.

Accordingly, much more is involved than forward displacement (homoeosis) of a single organ but rather a condition in which all organs of the cephalic region from gizzard posteriorly are three segments in front of their expected positions (regional homoeosis).

An initial or very early stage in an evolutionary development that may have reached its climax in the Puerto Rico and Panama worms is provided by *P. corethrurus*. In that species an intersegmental furrow between the first and second segments has disappeared along with the prostomium. The now rather flaccid fusion metamere is small. Proof of what happened is provided in many specimens by retention of the setae belonging to ii which are now near the first intersegmental furrow that morphologically is 2/3. With loss of those setae, as in some individuals of the species, the gizzard would have to be referred to v instead of vi. Organs behind the gizzard also would be one segment anterior to their usual position. Abortion of two further segments by the same process under way in *P. corethrurus* would provide the regional homoeoses of the Puerto Rico and Panama genera. Although body wall and associated nephridia were markedly reduced or deleted, the digestive system was not correspondingly shortened.

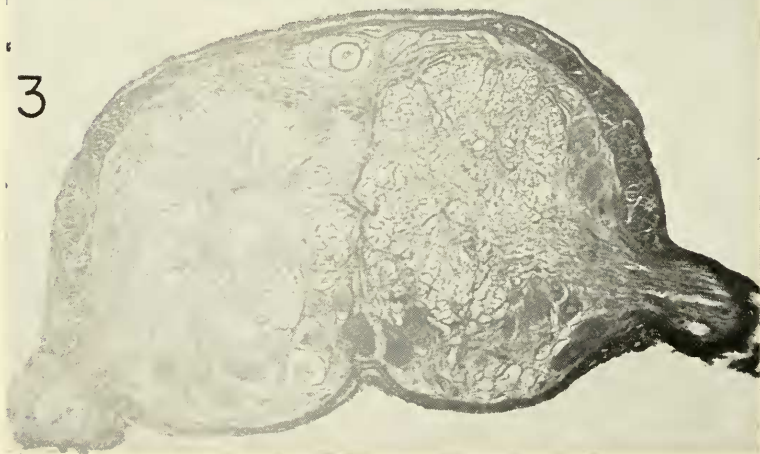
On the contrary, there has been so much elongation as to require very considerable enlargement of associated septa into posteriorly directed funnel-shapes. What happened in the nervous system may prove to be interesting also.

Although homoesoses are identical, the digestive systems and especially structure of the calciferous glands show that the two fore-shortened genera are not closely related. Puerto Rican worms may have evolved from a stock with calciferous glands in viii-x. Genera so characterized are unknown. Related forms should be sought to the south as the glossoscolecs evolved in tropical South America. Puerto Rico now appears to be the northern limit of generic endemism.

Completion of a development somewhat like that now under way in *P. corethrurus* may be responsible for attribution of testes in *Thamnodrilus matapi* Righi, 1969, to segments ix and x instead of the expected x and xi.

REFERENCES

- GATES, G. E. 1943. On some American and Oriental earthworms. Ohio Jour. Sci., 43: 97-116.
- . 1968. On a glossoscolecid earthworm from Panama and its genus. Megadrilogica, 1: 1-15.



LIST OF ILLUSTRATIONS

Figure 1. *E. montana*. Transverse section of nerve cord anteriorly to show muscularization of the sheath.

Figure 2. *E. montana*. Transverse section of nerve cord anteriorly to show the condition responsible for the appearance of a greyish translucent line at mD and mV.

Figure 3. *E. montana*. Transverse section of nerve cord anteriorly to show giant cells ventrally.